



Coupling between visual alpha oscillations and default mode activity[☆]

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ARTICLE INFO

Article history:

Accepted 29 November 2012

Available online 8 December 2012

Keywords:

Alpha oscillations
Default mode network
Simultaneous EEG-fMRI
Eyes-open
Eyes-closed

ABSTRACT

Although, on average, the magnitude of alpha oscillations (8 to 12 Hz) is decreased in task-relevant cortices during externally oriented attention, its fluctuations have significant consequences, with increased level of alpha associated with decreased level of visual processing and poorer behavioral performance. Functional MRI signals exhibit similar fluctuations. The default mode network (DMN) is on average deactivated in cognitive tasks requiring externally oriented attention. Momentarily insufficient deactivation of DMN, however, is often accompanied by decreased efficiency in stimulus processing, leading to attentional lapses. These observations appear to suggest that visual alpha power and DMN activity may be positively correlated. To what extent such correlation is preserved in the resting state is unclear. We addressed this problem by recording simultaneous EEG-fMRI from healthy human participants under two resting-state conditions: eyes-closed and eyes-open. Short-time visual alpha power was extracted as time series, which was then convolved with a canonical hemodynamic response function (HRF), and correlated with blood-oxygen-level-dependent (BOLD) signals. It was found that visual alpha power was positively correlated with DMN BOLD activity only when the eyes were open; no such correlation existed when the eyes were closed. Functionally, this could be interpreted as indicating that (1) under the eyes-open condition, strong DMN activity is associated with reduced visual cortical excitability, which serves to block external visual input from interfering with introspective mental processing mediated by DMN, while weak DMN activity is associated with increased visual cortical excitability, which helps to facilitate stimulus processing, and (2) under the eyes-closed condition, the lack of external visual input renders such a gating mechanism unnecessary.

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Introduction

Field oscillations in the alpha range (8–12 Hz) are a prominent feature of human electroencephalogram (EEG) over the occipital-parietal cortex. The genesis and function of alpha have been the subject of intense study since the 1920s (Berger, 1929; Bollimunta et al., 2008, 2011; Lopes da Silva, 1991; Shaw, 2003). It is generally believed that for a given brain state (e.g., attention versus relaxed wakefulness), the magnitude of alpha is an inverse indicator of cortical excitability, with smaller alpha associated with improved visual processing. Goal-oriented increase of alpha over task-irrelevant cortices, therefore, has been interpreted as reflecting a mechanism of active inhibition (Jensen et al., 2002; Klimesch, 1996). In tasks demanding externally-oriented attention, alpha power, on average, is reduced over task-relevant cortices (Rajagovindan and Ding, 2010; Sauseng et al., 2005). Momentary increase of alpha power over these task-relevant cortices is indicative of decreased level of attention and worsened task performance (Macdonald et al., 2011).

A recent study examining the neural signature of attention lapses has found increased alpha band oscillation up to 20 s prior to the occurrence of an error (O'Connell et al., 2009).

The level of BOLD activity in the default mode network (DMN), a key system mediating introspective processes such as mind wandering (Christoff et al., 2009; Mason et al., 2007), appears to exhibit behavior similar to that of alpha. It is suppressed or deactivated on average when subjects are actively engaged in demanding cognitive tasks (Buckner et al., 2008). Stronger deactivation of the DMN is associated with greater activation of the sensory cortices (Greicius and Menon, 2004). Attentional lapses, characterized by ineffective stimulus processing and decreased task performance, are associated with momentarily insufficient deactivation of the DMN (Eichele et al., 2008; Weissman et al., 2006).

Based on these functional data, it seems reasonable to expect that alpha power and DMN activity be positively correlated, and this property should persist even in the absence of tasks (resting-state). This hypothesis has been subjected to experimental test using the simultaneous EEG-fMRI technique. Despite repeated attempts (Goldman et al., 2002; Laufs et al., 2003a,b, 2006; Moosmann et al., 2003), however, supporting evidence remains lacking. A closer examination of the literature suggests one possible reason, namely, resting-state data were often recorded with the eyes closed. Such data may not be ideally suited to model observations made under conditions of active

[☆] No conflict of interest.

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visual processing. From a functional standpoint, positive alpha and DMN BOLD correlation, implying concurrent increase and decrease of alpha power and DMN BOLD, may serve to gate out sensory input to protect introspective processes from external interference. This protection is only necessary in the presence of visual input. Moreover, the act of opening the eyes has physiological consequences, including some reorganization of brain network activity. In particular, it has been shown that eyes-opening (1) suppresses alpha (Berger, 1929; Moosmann et al., 2003) and (2) increases functional connectivity within DMN (Yan et al., 2009).

In this study we sought to examine the relationship between occipital alpha oscillations and DMN activity by recording simultaneous EEG-fMRI in two types of resting-state sessions: a more traditional eyes-closed session and a less traditional eyes-open session. Alpha power fluctuations were extracted from visual EEG channels using short-time Fourier transforms and convolved with a canonical hemodynamic response function (HRF). The HRF-convolved alpha power time series was then correlated with the concurrent BOLD activity to assess their coupling.

Methods

Experimental procedure and data acquisition

Fourteen healthy college students with normal or corrected-to-normal vision participated in the study in exchange of course credit. The experimental protocol and data acquisition procedure were approved by the Institutional Review Board of the University of Florida. Prior to experiment, written informed consent was obtained from all participants.

The experiment consisted of two resting-state fMRI sessions each lasting 7 min. Participants were instructed to remain still, stay awake, not to think any systematic thoughts, and keep their eyes closed during one session. During the other session, they were asked to open their eyes and fixate on a fixation cross presented at the center of an MR-compatible monitor, and the instructions were otherwise the same. The order of the two sessions was randomized across participants.

EEG acquisition

EEG data were recorded using a 32-channel MR-compatible EEG system (Brain Products GmbH). Thirty one sintered Ag/AgCl electrodes were placed according to the 10–20 system and one additional electrode was placed on the participant's upper back to monitor electrocardiogram (ECG). ECG was used subsequently to aid the removal of the cardioballistic artifact. The impedance from all scalp channels was kept below 10 k Ω during the entire recording session as recommended by the manufacturer. The online band-pass filter had cutoff frequencies at 0.1 and 250 Hz. The filtered EEG signal was then sampled at 5 kHz, digitized to 16-bit, and transferred to the recording computer via a fiber-optic cable. The EEG recording system was synchronized with the scanner's internal clock throughout the recording session. The synchronization, along with the high sampling rate, was essential to ensure the successful removal of the gradient artifact.

fMRI acquisition

Functional images were acquired on a 3-Tesla Philips Achieva whole-body MRI system (Philips Medical Systems, Netherlands) using a T2*-weighted echoplanar imaging (EPI) sequence (echo time (TE) = 30 ms; repetition time (TR) = 1980 ms; flip angle = 80°). Two hundred and twelve (212) volumes of functional images were acquired during each experimental session, with each whole-brain volume consisting of 36 axial slices (field of view: 224 mm; matrix size: 64 × 64; slice thickness: 3.50 mm; voxel size: 3.5 × 3.5 × 3.5 mm). A T1-weighted high resolution structural image was obtained for each subject after the two resting-state sessions.

Data preprocessing

Dataset from two participants was excluded as they self-reported of falling asleep during at least one of the sessions. The final dataset analyzed in this study contained 12 participants (5 females; mean age: 22.9 ± 4.54).

EEG data

There were two sources of artifacts in EEG data specifically associated with simultaneous acquisition: gradient and cardioballistic. The gradient artifact was removed by subtracting an average artifact template from the EEG data as implemented in Brain Vision Analyzer 2.0 (Brain Products GmbH). The gradient artifact template was constructed by using a sliding-window approach which involved averaging the EEG signal across 41 consecutive volumes. The cardioballistic artifact was removed by an average artifact subtraction method proposed in Allen et al. (1998). In this method, the R peaks were detected in the ECG recordings in a semiautomatic way and then utilized to construct a delayed average artifact template over 21 consecutive heartbeat events. The cardioballistic artifact was then removed by subtracting the average artifact templates from the EEG data. After these two steps, the EEG data were then band-pass filtered between 0.5 and 50 Hz, down-sampled to 250 Hz, and re-referenced to the average reference. The MR-corrected EEG data were then exported to EEGLAB (Delorme and Makeig, 2004) to correct for eye-blinking, residual cardioballistic, and movement-related artifacts using SOBI (Second Order Blind Identification; Belouchrani et al., 1993). Recent work has shown that SOBI was effective in removing the cardioballistic artifact (Vanderperren et al., 2010), as well as in separating EEG data into interpretable neural components (Klemm et al., 2009; Tang et al., 2005).

fMRI data

fMRI data preprocessing was performed in SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/>). The first 5 scans of each session were discarded in order to eliminate the transient effects. Other preprocessing steps included slice timing, motion correction, normalization to the Montreal Neurological Institute (MNI) template, and re-sampling of the functional images into a voxel size of 3 × 3 × 3 mm³ (Friston et al., 1995). Normalized images were spatially-smoothed by using an 8 mm FWHM (Full Width at Half Maximum) Gaussian kernel. Global scaling was applied to remove the global signal from the BOLD time series. The BOLD time series was then high-pass filtered with a cutoff frequency at 1/128 Hz.

Estimation of alpha power time series

The scalp EEG voltage data from the three occipital channels O1, O2, and Oz were selected. The overall average power spectra for the eyes-closed session and for the eyes-open session were obtained using the Welch's method. The alpha power time series from each subject was extracted as follows. First, EEG signals for each channel were segmented into 500 ms non-overlapping epochs. Second, the EEG power spectrum for each single epoch was calculated using a nonparametric multitaper approach (Mitra and Pesaran, 1999), and the alpha band power was obtained by integrating the power spectrum between 8 and 12 Hz. Epochs that contained motion or muscle artifacts were interpolated using adjacent epochs. Third, the channel-level alpha power time series from each of the three occipital channels was averaged to yield the subject-level alpha power time series, which was convolved with a canonical hemodynamic response function (HRF). The HRF-convolved alpha power time series was then downsampled to the same sampling frequency as the BOLD signal, and normalized by 1) subtracting the mean and 2) dividing the mean-removed data by its standard deviation.

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